Theor Appl Genet (1988) 75:410–414

# Selection response and efficiency of doubled-haploid recurrent selection in a cross-fertilized species*

**T. M. Choo** [1] **and L. W. Kannenberg** [2]

[1] Agriculture Canada Research Station, Charlottetown, Prince Edward Island C1A 7M8, Canada
[2] Department of Crop Science, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Received March 6, 1987; Accepted June 25, 1987
Communicated by K. Sittmann

**Summary.** Computer simulation was used to compare the simulated response to doubled-haploid (DH) mass selection with the response predicted by mathematical formulae. The efficiency of DH versus diploid mass selection in a cross-fertilized species was also studied by means of theoretical consideration and computer simulation. Simulated gain was in agreement with the predicted gain in the DH population under both additive and complete dominance models. The simulated variance of response to DH mass selection was close to the predicted variance at both the 5% and 25% selection regimes under additive and complete dominance models. The efficiency of DH over diploid mass selection was shown to be dependent upon the allelic frequency, the degree of dominance, and the amount of environmental variance. In theory the efficiency can range from zero to infinity, but in reality it should be greater than one. The efficiency ranges from $\sqrt{2}$ to 2 in the absence of dominance; it can be greater than two only in the presence of dominance and a small environmental variance. The variance of response to DH mass selection can be smaller than or up to twice as large as the variance of response to diploid mass selection. Computer simulation results agreed with the predicted efficiency of DH mass selection and with the predicted variance-of-response ratio of DH mass selection to diploid mass selection.

**Key words:** Computer simulation – Doubled haploids – Response to selection – Mass selection

## Introduction

Haploids can be obtained by anther culture in many cross-fertilized species including maize and *Brassica* (Vasil 1980). Chase (1952) suggested that doubled haploids may prove useful as an adjunct to recurrent selection in maize. Griffing (1975) showed that if cycle lengths are equal, doubled haploid (DH) could be up to six times more effective than diploid selection procedures. Choo and Kannenberg (1978), using computer simulation, showed that DH mass selection was about 1.4 times faster than diploid mass selection and equal to $S_1$ selection in terms of gain per year.

Mathematical formulae for predicting mean and variance of response to selection have been developed (Baker 1971; Empig et al. 1972; Hill 1974). In a computer simulation study on a diploid cross-fertilized species, Choo and Kannenberg (1981) found that predicted gain for diploid mass selection was in agreement with simulated gain under an additive model but not under a complete dominance model, and that the predicted variance of response to mass selection appeared to be in agreement with the simulated variance under both genetic models. However, the accuracy of the mathematical formulae for predicting mean and variance of response to DH mass selection in a cross-fertilized species is not known.

The objectives of this study were: (1) to compare the predicted response to DH mass selection with the simulated response in a diploid, cross-fertilized species, and (2) to compare the mean and variance of response to DH mass selection with the mean and variance of response to diploid mass selection.

## Theory

Consider that doubled haploids are extracted from plants of a random-mating population of a diploid,

---

* Joint Contribution from the Charlottetown Research Station, contribution no. 604 and Department of Crop Science, University of Guelph

cross-fertilized species. M doubled-haploids are tested with one replication in the field and N doubled-haploid plants are selected on the basis of their phenotypic value. Open-pollinated progeny of selected plants are used to produce doubled haploids for the next selection cycle. Thus, selection is applied only to female parents. In each subsequent cycle, M doubled-haploids are produced and N plants are selected. The predicted mean response to selection for this DH population ($\Delta$G) can be expressed as follows:

$$\Delta \mathrm{G} = \mathrm{K}\, \sigma_{\mathrm{a}}^2/\sigma_{\mathrm{I}}$$

where $\sigma_{\mathrm{a}}^2$ is the additive genetic variance, $\sigma_{\mathrm{I}}$ is the phenotypic standard deviation of the DH population, and K is the standardized selection differential (see Empig et al. 1972 and Griffing 1975 for rationale). The predicted variance of response to selection for the DH population ($\sigma_{\Delta \mathrm{G}}^2$) can be expressed as follows:

$$\sigma_{\Delta \mathrm{G}}^2 = \frac{2\,\sigma_{\mathrm{a}}^2}{\mathrm{M}} + \frac{2\,\sigma_{\mathrm{a}}^2}{4}\left[\frac{1}{\mathrm{M}} + \frac{1-(1-\mathrm{k_p})\,\mathrm{h_I^2}}{\mathrm{N}}\right] + \frac{\sigma_0^2}{\mathrm{M}}$$

where $\mathrm{k_p}$ is a value associated with variances of order statistics ($\mathrm{k_p} = 0.30$ for 5% selection intensity and $\mathrm{k_p} = 0.51$ for 25% selection intensity), $\mathrm{h_I^2}$ is the narrow-sense heritability in the DH population, and $\sigma_0^2$ is the phenotypic variance of the DH offspring population (see Baker 1971 and Hill 1974 for rationale).

Suppose that mass selection is also conducted in a diploid population in an identical manner and under identical conditions. The only difference between DH and diploid mass selections is that the former involves testing and selection of doubled haploids, the latter testing and selection of diploids. The mathematical formulae for predicting mean and variance of response to mass selection in a diploid population were given by Choo and Kannenberg (1981). The efficiency of DH mass selection relative to diploid mass selection (E), or ratio of genetic gains, can be shown to be twice the ratio of diploid phenotypic standard deviation ($\sigma_{\mathrm{II}}$) to DH phenotypic standard deviation if dominance is absent or if, in the presence of dominance, allelic frequencies are equal to one-half, i.e.,

$$\mathrm{E} = 2\,\sigma_{\mathrm{II}}/\sigma_{\mathrm{I}} = 2\sqrt{\sigma_{\mathrm{a}}^2 + \sigma_{\mathrm{d}}^2 + \sigma_{\mathrm{e}}^2}\,/\sqrt{2\,\sigma_{\mathrm{a}}^2 + \sigma_{\mathrm{e}}^2}$$

where $\sigma_{\mathrm{d}}^2$ and $\sigma_{\mathrm{e}}^2$ are the dominance variance and the environmental variance, respectively. With no dominance, the efficiency is equal to $\sqrt{2}$ if the environmental variance is zero (i.e. heritability = 1), while it approaches two as the environmental variance approaches infinity (i.e. heritability $\doteq$ 0). The efficiency can be larger than two only in the presence of dominance and a small environmental variance. In theory, the efficiency can range from zero to infinity if allelic frequencies are not equal to one-half and dominance is present. Let p be the frequency of the dominant allele, q be the frequency of the recessive allele, 2 a be the difference between two homozygotes, and d be the deviation of the heterozygote from the mid-parent. If the environmental variance is equal to zero and the population is in equilibrium, the efficiency formula for a one-locus system can be rewritten as follows:

$$\mathrm{E} = \sqrt{4\,\mathrm{p\,q\,a^2}}\,\sqrt{2\,\mathrm{p\,q}\,[\mathrm{a} + \mathrm{d}\,(\mathrm{q} - \mathrm{p})]^2 + (2\,\mathrm{p\,q\,d})^2}\,/\,\{2\,\mathrm{p\,q}\,[\mathrm{a} + \mathrm{d}\,(\mathrm{q} - \mathrm{p})]^2\}.$$

**Table 1.** Effects of allelic frequency and degree of dominance on the efficiency of DH mass selection over diploid mass selection, assuming $\sigma_{\mathrm{e}}^2 = 0$ and a = 1

| Allelic frequency | Efficiency | | | |
|---|---|---|---|---|
| | d = 1 | d = 2 | d = −1 | d = −2 |
| p = 0.01, q = 0.99 | 0.06 | 0.48 | 507.48 | 1.54 |
| p = 0.10, q = 0.90 | 0.63 | 0.57 | 16.58 | 4.08 |
| p = 0.50, q = 0.50 | 1.73 | 2.45 | 1.74 | 2.45 |
| p = 0.90, q = 0.10 | 16.58 | 4.08 | 0.63 | 0.57 |
| p = 0.99, q = 0.01 | 507.47 | 1.54 | 0.06 | 0.48 |

The efficiency can be studied by assigning different values of p, a and d (Table 1). DH mass selection is more efficient than diploid mass selection if the frequency of dominant desirable alleles exceeds 0.5 (Choo and Kannenberg 1978, Fig. 3) or if the frequency of recessive desirable alleles is less than 0.5. This observation differs from the one by Griffing (1975), who reported that the efficiency of DH mass selection is increased when the frequency of dominant desirable allele is less than 0.5, or when the frequency of recessive desirable allele is greater than 0.5. This theoretical consideration illustrates that the efficiency of DH over diploid mass selection is dependent upon the allelic frequency, the degree of dominance, and the amount of environmental variance. In reality, the expression of most quantitative traits in different species is affected by environment. Many quantitative traits have a low heritability in actual selection programs. Therefore, DH mass selection is most likely more efficient (i.e., E > 1) than diploid mass selection.

Assume that the genetic variance of the offspring population is the same as that of the parental population, and that the environmental variance is constant from cycle to cycle. Then, the variance-of-response ratio of DH mass selection to diploid mass selection (VR) can be described as follows:

$$\mathrm{VR} = \frac{4\,\mathrm{N}\,(4\,\sigma_{\mathrm{a}}^2 + \sigma_{\mathrm{e}}^2) + 2\,\sigma_{\mathrm{a}}^2\,\{\mathrm{N} + \mathrm{M}\,[1-(1-\mathrm{k_p})\,\mathrm{h_I^2}]\}}{4\,\mathrm{N}\,(2\,\sigma_{\mathrm{a'}}^2 + \sigma_{\mathrm{d}}^2 + \sigma_{\mathrm{e}}^2) + \sigma_{\mathrm{a'}}^2\,\{\mathrm{N} + \mathrm{M}\,[1-(1-\mathrm{k_p})\,\mathrm{h_{II}^2}]\}}$$

where $\sigma_{a'}^2$ and $h_{II}^2$ are the additive genetic variance and the narrow-sense heritability in the diploid population, respectively. With no dominance, the variance ratio is equal to two if the environmental variance is zero, while it approaches one as the environmental variance approaches infinity. The variance ratio is less than one only in the presence of dominance and a small environmental variance. Thus, the variance ratio formula shows that the variance of response to DH mass selection: (1) is at most twice as large as the variance of response to diploid mass selection, (2) is 1 to 2 times larger than the variance of response to diploid mass selection in the absence of dominance, and (3) is smaller than the variance of response to diploid mass selection only in the presence of dominance and a small environmental variance.

## Simulation model

Methods for simulating mass selection in both DH and diploid populations have been reported previously (Choo and Kannenberg 1978). Simulated selection in both DH and diploid populations began with 20 parents. The initial DH population was developed by doubling the chromosome number of 400 haploids (20 random haploids from each of 20 parents). In the initial diploid population, 20 progeny were taken from each of the 20 parents. Subsequently, the 20 (5%) and 100 (25%) plants, respectively, with the highest phenotypic values were selected in each cycle. The 400 population size in both the DH and diploid populations was restored in each cycle by taking from each selected plant 20 diploid or DH progeny for the 5% selection intensity regime, and four diploid or DH progeny for the 25% selection intensity regime. Pollination was assumed to be at random. Selection was applied for 30 cycles only to the female parents.

The character under selection was controlled by 20 major and 20 minor genes. The effect of a major gene ($a = 2$) was twice that of a minor gene ($a = 1$). The frequency of desirable alleles in the ancestral population was 0.5 for ten of the major and ten of the minor genes, and 0.1 for the remaining ten of both types. Environmental deviations were assumed to be normally distributed with zero mean and an environmental variance of 136 under an additive model, or of 203 under a complete dominance model. The environmental variances were equivalent to a narrow-sense heritability of 0.2 in the ancestral parental population, and were kept constant in each cycle in each selection regime. Two computer runs were conducted in each selection regime.

The procedures for calculating the predicted and simulated responses to diploid mass selection have been reported previously (Choo and Kannenberg 1981). Therefore, only those for calculating the predicted and simulated responses to DH mass selection are described here. The phenotypic and genotypic variances were calculated by the conventional statistical method. The averages of genotypic and phenotypic variances from the two runs were used to calculate the predicted mean and variance of response for each selection cycle. A total of 30 predicted means and variances of response was obtained in each regime. The averages of the 30 predicted variances are given in Table 2. The simulated responses to selection for the 30 cycles were also calculated from the selection gains of the two runs.

In this simulation model, DH mass selection was predicted to be more efficient than diploid mass selection in early selection cycles when the genotypic variance of the DH population was not yet exhausted (Table 3). DH mass selection was also predicted to have a larger variation of response than diploid mass selection (Table 3). To check the prediction, the simulated mean and variance of response to the two types of mass selection were calculated. Because response to DH mass selection reached a plateau in later cycles (Choo and Kannenberg 1978), the simulated efficiency was calculated on the basis of the average of selection gains of the first 15 cycles for both types of mass selection. The simulated variance-of-response ratio was calculated by dividing the average of 30 variances of response to DH mass selection by the average of 30 variances of response to diploid mass selection.

**Table 2.** The predicted and simulated variances of response to DH mass selection under additive and complete dominance models (assumed heritability: 0.2)

| Genetic model | Selection intensity (%) | Predicted variance | Simulated variance |
|---|---|---|---|
| Additive | 5 | 0.88 | 1.21 |
| Additive | 25 | 0.72 | 1.16 |
| Dominance | 5 | 1.11 | 1.13 |
| Dominance | 25 | 0.90 | 1.36 |

**Table 3.** The efficiency and variance-of-response ratio of DH mass selection over diploid mass selection under additive and complete dominance (assumed heritability: 0.2)

| Genetic model | Selection intensity (%) | Efficiency | | Variance-of-response ratio | |
|---|---|---|---|---|---|
| | | Predicted | Simulated | Predicted | Simulated |
| Additive | 5 | 1.83 | 1.53 | 1.10 | 1.56 |
| Additive | 25 | 1.83 | 1.84 | 1.22 | 2.45 |
| Dominance | 5 | 1.26 | 1.34 | 1.00 | 1.07 |
| Dominance | 25 | 1.26 | 1.35 | 1.09 | 1.71 |

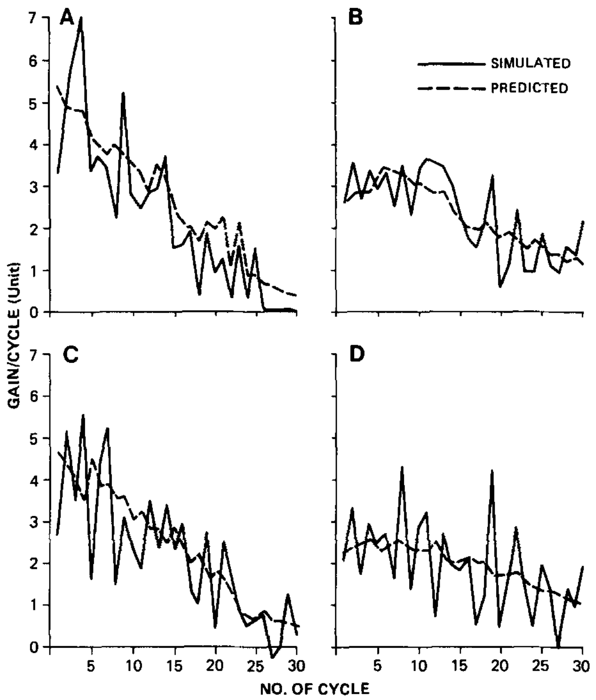

**Fig. 1 A – D.** Computer simulated and predicted gains during 30 cycles of doubled-haploid mass selection under an additive and a complete dominance model (computer simulated and predicted gains were the averages of two runs). **A** At 5% selection under an additive model. **B** At 25% selection under an additive model. **C** At 5% selection under a complete dominance model. **D** At 25% selection under a complete dominance model

## Results and discussion

The simulated and predicted gains over 30 cycles of DH mass selection were in agreement for each of the two selection regimes under the additive and complete dominance models (Fig. 1). As expected, the simulated gain fluctuated in a zigzag pattern along the trend of the predicted gains over selection cycles. The extent of fluctuation was smallest with the 25% selection regime under the additive model. Negative response to selection was found in the 30th cycle of the 5% selection regime under the additive model, and in the 27th cycle of both the 5% and 25% selection regimes under the complete dominance model. In the earlier cycles, the gain per cycle ranged from 7% of the initial population mean at the 25% selection regime under the complete dominance model to 12% at the 5% selection regime under the additive model. The gain per cycle was smaller in the advanced cycles, especially for the 5% selection regime under the additive model, due to reduced genotypic variability. The simulated variance was very close to the predicted variance for each selection regime under both genetic models (Table 2).

The predicted efficiency of DH over diploid mass selection was 1.83 and 1.26 under the additive and complete dominance models, respectively. The simulated and predicted efficiencies were in agreement for each selection regime under the two genetic models (Table 3). The simulated variance-of-response ratio of DH to diploid mass selection was quite similar to the predicted one (Table 3).

In this study, computer simulation results demonstrated that the mathematical formulae for predicting mean and variance of response to DH mass selection were accurate. The formula for predicting mean response was based on these assumptions: random mating population in equilibrium, diploid pairing at meiosis, no linkage, no multiple alleles, and no epistasis (Empig et al. 1972). The computer simulation model met all these assumptions. But in the advanced cycles, genetic disequilibrium could be built up by selection with or without linkage (Choo and Kannenberg 1981). These results suggest that the predicting formulae for DH mass selection can be applied to a population in genetic disequilibrium.

The simulated and predicted gains were in agreement under the additive and complete dominance models in this study. However, a previous study by Choo and Kannenberg (1981) showed that the simulated and predicted gains for diploid mass selection were in agreement only under the additive (but not under the complete dominance) model. The discrepancy between DH and diploid mass selections under the complete dominance model (Choo and Kannenberg 1981) is due to the fact that the genotypic variance of the DH population (= twice the amount of additive genetic variance) was calculated by the conventional statistical method, while the additive genetic variance of the diploid population was estimated by a formula based on gene frequency. In this study, the selection response to DH mass selection was higher under the additive model than under the complete dominance model; this is because the enviromental variance is smaller under the additive model.

The simulated efficiency of DH over diploid mass selection was very close to its prediction for each regime under both genetic models. In addition, the simulated variance-of-response ratio was quite similar to the predicted ratio. This suggests that the efficiency and the variance ratio formulae for comparing the relative performance between DH and diploid mass selections are accurate. Although the formulae were developed for mass selection where only females are selected, the formulae also apply to mass selection where both males and females are selected. If the selection procedures and conditions are identical for both DH and diploid populations, the formulae also apply to the clonal selection procedure (Griffing 1975) because the clonal selection procedure aims only at reducing environmental variance by replication.

## References

Baker RJ (1971) Theoretical variance of response to modified pedigree selection. Can J Plant Sci 51:463–468

Chase SS (1952) Production of homozygous diploids of maize from monoploids. Agron J 44:263–267

Choo TM, Kannenberg LW (1978) The efficiency of using doubled haploids in a recurrent selection program in a diploid, cross-fertilized species. Can J Genet Cytol 20: 505–511

Choo TM, Kannenberg LW (1981) Comparison of predicted and simulated responses to mass selection in a diploid, cross-fertilized species. Can J Plant Sci 61:1–8

Empig LT, Gardner CO, Compton WA (1972) Theoretical gains for different population improvement procedures. Univ Nebraska Agric Exp Stn Bull Misc Publ 26 (revised)

Griffing B (1975) Efficiency changes due to use of doubled-haploids in recurrent selection methods. Theor Appl Genet 46:367–386

Hill WG (1974) Variability of response to selection in genetic experiments. Biometrics 27:293–311

Vasil IK (1980) Androgenetic haploids. In: Vasil IK (ed) Perspectives in plant cell and tissue culture. Academic Press, New York, pp 195–223